ORTHOGENESIS IN BACTERIA

PROFESSOR CHAS. B. LIPMAN

UNIVERSITY OF CALIFORNIA

It is well to understand at the outset that bacteria, unlike plants and animals, can not be studied from the orthogenetic standpoint in the strict sense, owing to the lack of a proper vantage point, or, perhaps more correctly speaking, a basis from which one may start such a study. In my opinion, all attemps at the establishment of systems of bacteria, and there have been many, have ended in creating greater confusion than there was at the start. Such frustration of well-intentioned programs was inevitable for at least three reasons, to wit: (1) Every bacteriologist used criteria of his own for the establishment of new species. This is bound to lead to chaos. (2) Nearly all bacteriologists used a morphological basis for classification. Owing to the relative simplicity of form of bacteria, this must inevitably result in erroneous discriminations. (3) Nearly all bacteriologists in the past and even to-day are laboring under the misconception that bacteria are simpler forms of living organisms than they really are. That this is incorrect has been shown by the studies of Löhnis and Smith in 1916[1] and of Löhnis alone very recently.[2]

But assuming the foregoing to be true, it must follow that it is impossible to trace the evolution of new species of bacteria in a definitely directed course. Not being certain what constitutes a forward or what a backward step

[1] (*a*) "Life Cycles of the Bacteria," preliminary communication, *Jour. Agric. Res.*, Vol. 6, No. 18. (*b*) "Life Cycles of the Bacteria," paper read at New Haven meeting of Soc. Amer. Bacteriologists, Dec. 27, 1916.

[2] "Studies upon the Life Cycles of the Bacteria," Part I, Review of the Literature, 1838–1918, *Nat. Acad. Sciences*, Vol. XVI, Second Memoir.

in bacterial development, it is obvious that we can not apply as justifiably as we do in the case of the higher organisms the criteria of definitely directed evolution. To be sure, we have a number of instances of the establishment of permanent new characters in bacteria, yeasts, and other fungi through the influence of a change in environment. Most of these are, however, induced through changes in the medium under artificial conditions and they do not necessarily indicate a change in the direction of improvement of the organism or of greater complexity in its organization which may in turn point to the evolution of a higher form from a lower one.

Despite the foregoing, it is probably well to examine into certain facts with which we are familiar with regard to microorganisms, and which may, perhaps, have a close bearing upon what might be regarded as orthogenesis in bacteria. The first fact to which I wish to refer is that of parasitism. There can probably be very little doubt that parasitism on the part of bacterial cells is not an original, but an acquired character, using the term "acquired" in its literal, and not technical, sense. If that is granted, it would also follow that the acquirement of such a characteristic by a microorganism would mean the gradual adaptation of a bacterial cell from one kind of a medium to another. It would mean the gradual acquirement of partiality on the part of a microorganism towards certain chemical substances, certain temperatures, or certain other conditions which obtain only in a living host and not in an inanimate medium. The steps, gradual or rapid, by which the acquirement of such peculiar characteristics on the part of the microorganism would occur in its change from a saprophyte to a parasite would almost seem to imply evolution in a definite direction. In a sense, therefore, we may regard parasitism in bacteria as an evidence of orthogenetic development in such organism. It is, moreover, a case of evolution in a definite direction through the influences of environmental factors of the natural order and not those

which are produced artificially. In respect, therefore, of causal factors in the evolution of bacteria, we have parasitism exemplifying the antithesis, so to speak, of changes which we induce in bacteria in our artificial media, or by changes in the environment. These observations would seem to possess cogency, not only in the case of obligate parasitism, such as that characterizing the organism of human tuberculosis, or of anthrax, or of the fungus of wheat rust, but also that of what we may call facultative parasitism in which the organism may have adapted itself to life, both as a saprophyte and as a parasite through the influence of certain chemical or physical-chemical agencies in its environment which have rendered its protoplasm more highly adaptable than that of the obligate parasite. We may, therefore, regard facultative parasitism as an instance of orthogenetic evolution, just as we may so regard obligate parasitism. The puzzling question which may, however, arise, from these considerations is, which is the more advanced step in orthogenesis in parasitic bacteria. Is the obligate parasite the more advanced form, or is the facultative parasite the more advanced form? While many would probably, on first impulse, regard the former as the correct answer, it does not necessarily follow that such is the case. Certainly in this regard, a great many more facts are needed before any definite statements can be made.

Examples of other cases of orthogenetic evolution in bacteria other than the case of parasitism, which I have just discussed, may be multiplied *ad libitum*. But, owing to limitations of time and space, it will suffice to mention a few only.

The adaptation of bacteria to the physiological characteristic of nitrogen fixation, such as is possessed by all the *Azotobacter* species, and the *Clostridium* species and, to a slight extent, by many other species, can scarcely have been the result of anything else than a case of definitely directed evolution. This was probably accomplished through the influence of an environment in which

it was impossible for the organisms existing therein to live without acquiring a power of employing energy existent in carbonaceous material to fix atmospheric nitrogen and make it available for their own life processes. The next case which may be cited is that of the lactic-acid bacteria, which possess the power of transforming lactose (or milk sugar) into lactic acid. These cells are not in form or otherwise in function appreciably different from any other bacteria with which we are acquainted. They have, nevertheless, this specific and peculiar power to which I have alluded. Is it likely that they have acquired this power through any other influence than the influence of environment which operated in a definite direction and hence orthogenetically? The sulphur bacteria, or particularly those species of sulphur bacteria which have the power of oxidizing sulphur to sulphuric acid, are another case in point. The nitrifying bacteria are still another case in point. The iron oxidizing bacteria are still another case, and so we might go on and mention very many classes of bacteria, in each case of which there is a definite, distinct, and strikingly peculiar functional power which could not well have been developed without the influence of some environmental factor or factors operating in a definite direction. It is not so easy on the morphological side to give examples like those which I have just cited from the point of view of function of the bacteria. The reason for that has already been touched on above, namely, the simplicity of form and particularly the slight variety in form which characterizes the bacteria. In fact, it is my conviction that it is best to ignore, largely, morphological factors in bacteria when we study the problem of bacterial evolution. My conviction arises from a study of many and varied experiments which I can not discuss here.

Viewing our subject, then, from the standpoint that orthogenesis in bacteria would be concerned with progressive changes in the organism, principally physiological, due to its response to changes in environment, it

seems that we must admit that orthogenesis does exist there. But if, on the other hand, progressive changes like those in question must also be in the direction of producing a more advanced form of organism, we are confronted by a quandary resulting from a lack of an accepted definition for the term "advanced."

The argument that bacteria do not *at all* lend themselves to appraisal as regards evolution by the standards applying to the higher organisms is, perhaps, not sound as shown again by the researches of Löhnis, which I have just cited. The objection to viewing bacteria in a manner similar to the higher organisms because no sexual reproduction is known among them is removed by Löhnis' observations, which indicate that something akin to a real conjugation of cells does occur in the bacteria. His striking monograph in the Memoirs of the National Academy should be read and studied by all those who seek new light on the origin and nature of bacteria.

Another point of view which I believe may be introduced into this discussion with some justification results from a broad comparison of natural phenomena generally. In the inanimate world, we are confronted by the evolution of substances in series in which the first member of the series is simple and by small accretions becomes progressively more complex in the succeeding members of the series until very complex materials are finally built up. We are all well acquainted with the seriation showing progressive complexity in the hydrocarbons beginning with methane and going up; in the carbohydrates beginning with formaldehyde and going up; in the proteins beginning perhaps with amino acids and going up. Such examples of progressive seriation may be multiplied *ad libitum*. Why, therefore, should it not be possible that similar series should arise in the progressive evolution of bacteria through certain forces as yet largely unknown which cause accretions of characters, so to speak, to occur in bacteria through their being rendered more complex and complicated by the influence of

certain factors of the environment. It seems inconceivable to me that the great diversity and complexity of functional nature in the bacteria could have arisen otherwise. Nevertheless, analogies between phenomena in animate and inanimate nature must not be pushed too far in the absence of the necessary facts for their support. While I believe them to be of great significance, I do not desire to be dogmatic on the subject in the slightest degree.

While all the foregoing as regards the evidence for orthogenesis may be accepted as true, it does not follow that the doctrine of orthogenesis is anything new or significant or was so when it was first enunciated. It seems to me to constitute merely one way of describing the actual condition of progressive series in evolution, but it seems to me that it *explains* nothing. In so far, however, as its advocates espouse the cause of those who believe in and give evidence for the inheritance of acquired characteristics, the potency of environment in inducing fundamental and permanent changes in the organism, and the theory of mutation, they do contribute something significant to the discussions and experiments which constitute the amorphous symplasm, metaphorically speaking, from which our knowledge of the well-defined and real nature and origin of life may some day be expected to emerge.

It is, perhaps, of particular importance now to consider the bacteria as a class and their probable origin as bearing on the question for which we are trying to find an answer. There is a general disposition, and particularly is it true that there has been in the past, on the part of biologists and natural philosophers, so called, to place the bacteria in point of origin among the most primitive of living organisms. There is much inclination, indeed, to regard them as *the* most primitive organisms. While, superficially, this view seems attractive and correct, it loses much of its cogency when one takes into consideration the following situation: In all but a few

exceptional forms of bacteria, some of which I have named above, the physiological characteristic is either that of a saprophyte or of a parasite. It seems obvious to me that neither a saprophytic nor a parasitic organism can well be expected to originate in an environment which is devoid of elaborated organic matter. Subject to considerations which I shall discuss later, we must, therefore, accept one or two conclusions with regard to the origin of bacteria in the scale of evolution of organisms generally. Either they are the most primitive forms of organisms which have lost their primitive powers of living in purely inorganic media, or they are a much more advanced form of life which came to be after other organic forms had for some time been developing on the earth's surface. The first possibility is merely tantamount to saying that some cells of the most primitive forms have gradually adapted themselves to either a saprophytic or a parasitic existence and, therefore, is of little assistance to us. The correctness of the second conclusion, however, would seem to depend on many little-known factors. Still, it is the belief of many scholars. Putting the matter in another way for greater clarity and emphasis, I may state it as the opinion of several plant physiologists who have speculated upon this subject, that the primitive forms of living cells were probably those which could live in a purely inorganic medium. Obviously, such cells must have been limited to the group which we now call the autotrophic organisms, and of the autotrophic organisms, since the higher plants are certainly a very advanced form, we must have had something very much simpler, and the natural conclusion is that such a simpler form of organism must have been the single-celled green alga, or forms closely similar to it. If we assume that such was the case, then it is not difficult to propose a scheme of evolution of the bacteria which involves the gradual change of the unicellular green algæ into a variety of bacterial forms through the influences of environmental factors as I have already in-

dicated. It is not at all inconceivable that a green algal cell may have adapted itself gradually to life within a higher plant cell or within an animal cell, or to a saprophytic existence in soil or other media devoid of light. It may first have come there accidentally and then, through the power to respond to such an environment and to tolerate it, has gradually evolved new powers and has lost some of its old powers. It is conceivable, therefore, that whether we regard parasites and saprophytes among the bacteria as degraded forms or not, they may be examples of evolution in a definite direction, presumably in this case in the direction of greater complexity of function resulting from the urge of a constantly and markedly changing and potent environment.

Since the foregoing observations on orthogenesis in bacteria have led me to enunciate in another form a theory accounting for the origin of bacterial forms which has been discussed before, I feel constrained to go one step farther into that subject in order that my own views may not be misunderstood. While the idea of accounting for the origin of the bacterial cell from the single-cell alga seems attractive and appears to be in consonance with certain well-known facts, there are several troublesome features about it. In the first place, it assumes the development of so complicated and intricate a substance as chlorophyll before any form of living substance was evolved. While this may, of course, have been the case, it seems doubtful, in view of what we must consider to be the highly specialized nature of the green pigment of plants. In the second place, we have seen that the strong argument in favor of the theory of the single-celled alga as the primordial cell, or rather against the theory that bacteria may have been such primordial cells, lies in the well-known fact that most bacteria require organic compounds as energy for their life processes and that no organic matter could have been available without the activity of chlorophyllous organisms. This argument, however, overlooks two points, viz., first, the existence of

autotrophic bacteria and, second, the possibility and even probability that sufficient amounts of organic matter for bacterial purposes may have been elaborated at the dawn of life by chemical means, using the term "chemical" in the broadest sense. It is, of course, well known that the autotrophic bacteria, for example, the nitrifying bacteria, can live and build organic matter out of purely inorganic substances, carbon being obtained from carbon dioxide of the air, and in the absence of light and chlorophyll. But if this is so, why may it not be that of the known forms of living cells, the autotrophic bacteria were the first, since they are capable of living in a purely inorganic medium, the ammonia which is necessary to them being supplied from the small amounts resulting from chemical reactions induced by electrical phenomena in the atmosphere. As we have seen thus far, it may be argued, with equal justice, that the activity of the nitrifying bacteria is a highly specialized one on the one hand, and a very primitive one on the other.

But if, as just indicated, it should be argued that, after all, the autotrophic bacteria are exceptions in the bacterial world and that most bacteria need elaborated organic matter and hence they could not have been the primordial living cells, the second objection which I have stated may be urged, namely, that organic matter may have existed on the earth before living cells came into being. Mature reflection will render it highly plausible with the high temperatures, great electrical activity, and probable intense radioactivity which existed on the planet prior to the appearance of living cells, that unusual chemical activity inducing rapid and general combinations among the elements should have prevailed. This, moreover, involves the assumption of the existence of a degree of all these conditions which is requisite for the synthesis, but not for the rapid destruction of the organic matter, which must also be conceded as probable. Under such conditions, it is reasonable to suppose that bacteria, on being evolved as the primordial cells, may

have found the conditions requisite to their growth and further development.

It seems, on careful deliberation, that strong arguments may be brought forward for both the theory that single-celled green algæ and the theory that bacteria were the primordial organisms, if we consider merely the arguments which enter into the usual discussions of the subject. But it appears to me that we must penetrate beyond what is ordinarily called careful deliberation, if we would see other possibilities for explaining the origin of living matter. There is no logical reason for confining our attention in these discussions to the single-celled algæ and the bacteria which we know. There are, in addition, bacteria so small as to challenge and defy our ingenuity for devising means for rendering them visible. What may not further discoveries about their nature and requirements for life unearth for us which may be of the most vital significance to the solution of our problem? I have tried in imagination to go beyond, far beyond, the ultramicroscopic bacteria and have pictured to myself the following condition for the origin of living matter: A single molecule of organic matter, let us say, a polypeptid or a proteid molecule produced by the force which I have discussed, exerted as chemical energy, may, in floating about in its aqueous medium on the earth's surface, suddenly find itself in a field of radioactive force or some similar force which causes its atoms to orient themselves in such fashion and to vibrate in such a manner as to endow it with certain activities which we now regard as attributes of life. Crude though this conception may be, it constitutes a step, though perhaps a very bold one, into the realm of possibilities for explaining the origin of the first living cell, a subject which we must consider together with all our theories of evolution if we do not wish to remove the inspiration to progress by arriving at an impasse in our theories and our hypotheses.

In conclusion, it is well to review briefly the discussion which I have just presented in a very brief form. Out

of regard for your time and patience, I have merely presented in outline each of the important considerations which I deem of direct significance to the question at issue. I have presented the difficulties which lie in the path of treating bacteria from the point of view of orthogenesis, and yet have shown that they may be so treated with certain justifiable assumptions as a basis. Having thus treated them, however, I have shown that whether the theory of orthogenesis holds for bacteria or not, it can not be considered as explaining anything, but merely as a mode of describing our observations. I have gone into the more fascinating and what seems to me to be the more useful discussion of the origins of living cells and the position of the bacteria with regard to such primordial cells. I have mentioned the various hypotheses which, in my opinion, may be considered to be the most plausible in that connection, and have shown the weaknesses and the strength of each. It has been my purpose to give an unbiased presentation of my own hypotheses and those of others without prejudice to any so that you might be enabled to discuss them all and arrive at your own conclusions. Without a thorough review of the literature of bacterial physiology and morphology, it is not easy to obtain a broad enough view of the subject to do it justice and I would urge particularly that those who are interested in it acquaint themselves with the absorbing and inspiring literature of the subject of mutation in microorganisms. I believe that it is full of significance for biological progress and I wish that circumstances made it possible for me to present a brief review of it for your consideration. As it is, I must content myself with directing your attention to it and with expressing the hope that my humble efforts in preparing and presenting this paper will constitute a step forward in our progress of thought and experimentation on problems in the evolution of living matter.